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Despite the plentiful navigation aids provided for our airplanes, poor visibility still presents major problems and hazards. Passengers and pilots alike feel isolated and somewhat "lost" when flying at night or in thick weather. Hence, it is only with a feeling of humility that one compares human air navigation to the bird migrations, which cover thousands of miles from the Arctic to the Tropics, without the aid of engines or instruments. Could our air navigation profit from a study of the methods employed by birds to guide their flight over trackless stretches of land or ocean? Before we can answer such a question, we must first know what the birds' methods really are.

First, it might be well to question why millions of birds bother to fly north at all. Why should they leave the temperate latitudes for the exertion and hazard of long annual migrations? Crowding, competition for nesting space, and even memories of ancestors who lived millions of years before--all of these factors have been suggested to account for the annual mass movement (Thompson, 1926).

Only recently another factor has attracted attention--the length of daylight, which depends directly on latitude. There have been few actual attempts to study this matter in the Arctic; hence, I should like to mention an observation which seems to be significant in this connection.

In 1948 scientists from Cornell made continuous observations of nesting birds, at Point Barrow, Alaska, for from 24 to 48 hours at a stretch. They found that in the continuous daylight of late June (69°23′ North latitude) robins brought food to the young during 21 hours of the day, resting for only three hours in the middle of the night when the temperature was just above freezing. In contrast, the same species (Turdus migratorius) in the northern United States feeds its nestling young for only about 16 hours a day. The arctic robins made an average of 137 feeding trips per day, compared to 96 made by the others. More important, the arctic birds matured faster--the brood observed left the nest 8.8 days after hatching, compared to an average of 14 days for the same species in the northern U.S. Now it is well known that the period when young birds must remain in the nest is one of the most dangerous in their lives, for they are helpless and readily located by enemies. Thus, it seems possible that shortening of the nestling period increases their chance of survival enough to justify the migration to the arctic latitudes; but further study is necessary to find a definite answer.

Donald R. Griffin (B. S and Ph. D. Harvard University) is well known for his studies on the use of ultrasonic sound by bats to guide themselves through darkness. His other research interests have included investigations of the physiology of protection from cold (in men and animals) and various aspects of physiological optics and acoustics. At present he is Associate Professor of Zoology at Cornell. He first presented the material contained in this article at a meeting of the Alaskan Science Conference held earlier this year.

Essentially the problem of bird navigation is a double one: first, to discover which of their senses tells birds the right direction for a migratory flight, and second, to find the environmental clue which provides the information (Griffin 1944). There is much disagreement about the sensory mechanism responsible for bird navigation. We know that in birds, vision is developed to a much greater extent than the other senses. Yet it cannot account for all bird navigation, for many migratory flights take place at night, through clouds, or even in fog.

One popular theory claims that birds are sensitive to the earth's magnetic field and guide their motions accordingly (Yeagley 1947), but there is little supporting evidence for this idea (Thorpe, et al 1949; Gordon 1948). Another hypothesis advances the idea that birds can perceive the mechanical forces resulting from the earth's rotation. There are enormous difficulties, however, in the way of a bird's being able to feel such effects.

Thus, there is little to encourage us in the many theories which suggest that some new "sense" accounts for bird migrations. But there are other explanations which credit bird navigation to clues perceived by the known sense organs. These theories, if valid, might offer more hope for application to human air navigation. For whatever a bird can see or feel might also be detectable by men.

In this connection we must first consider a theory which undoubtedly has some validity, though it does not provide a full explanation. This is the simple idea that birds rely on contact flying. We know that birds have performed amazing feats in remembering details of things they have seen. B. F. Skinner, for example, has trained ordinary domestic pigeons to peck at a specific object in an aerial photograph of a small area of ground with food as a reward. He found that even four years after their last observation, the birds were able to remember it well enough to peck immediately at the appropriate point, even though they had seen nothing in the meantime which even resembled the picture. This type of experiment should be extended to include photographs of terrain of interest to migrating birds; even now, however, there is enough evidence to show that birds have highly developed ability to remember the physical features of a landscape.

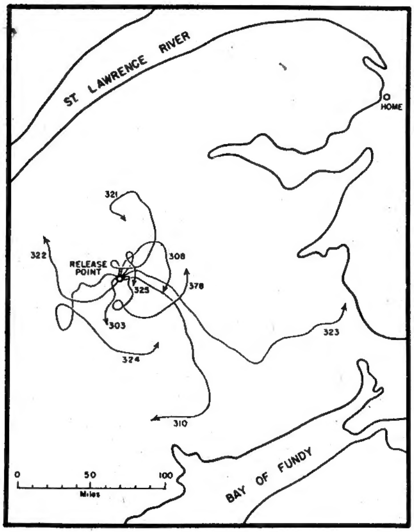


Figure 1. Actual flight paths of homing gannets released at Caribou showed that birds explored in all directions before reaching the coast and presumably familiar territory.

Another example of the importance of landmarks was indicated by experiments conducted in 1947 by R. J. Hock and the author. We were interested in the ability of birds to perform a sort of artificial migration after they are caught in their nests, carried in closed boxes

to territory unknown to them, and then set free. Many species have returned hundreds of miles in a few days after such sorties. A study of this type of navigation might help explain natural migrations.

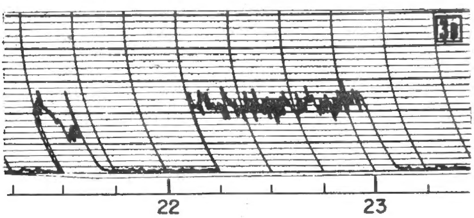
Figure 2. The author holds a long-billed dowitcher after attaching a radioactive tag to its left leg. The tag consists of an aluminum capsule less than 1/4-inch in diameter, with the radioactive material sealed into its center.

The gannet, a large white sea bird, which nests on an island in the Gulf of St. Lawrence was chosen for our first experiments. Seventeen of these birds were carried inland to northern Maine, a locale 215 miles from their nests, 100 miles from the nearest salt water and definitely new to them. After releasing the birds, we followed their flight in a small airplane in such a way that we could watch a particular gannet for hours at a time. We kept the plane 1500-2000 feet above the birds, which did not seem to be at all disturbed. We found that 62.5 percent of the birds returned home in from 1 to 4 days--a homing performance approximately equal to that of the several other wild species studied in the same way. Nine of the gannets were followed from the airplane for from 25 to 230 miles, while the remaining 8 were used as controls. The performance of the two groups was not appreciably different.

Figure 1, showing the paths of these birds, demonstrates graphically that the homing flight was not necessarily direct. Some birds which showed the most marked deviations nevertheless reached their nests within 2 to 3 days. Furthermore, mathematical analyses of more extensive homing experiments reveal that it is quite possible that other species which have returned from several hundred miles may also have found their way by exploration. Yet before airplane observations had been made it was almost universally believed that birds flew roughly straight home in such experiments--deviating no more than a few degrees from the direct path.

Gannets, however, are not among the birds which naturally carry out the longest and most impressive migrations. For this reason it might be argued that they simply did not display the highly developed powers of navigation characteristic of plovers and sandpipers, for example. To obtain evidence on this comparative aspect of bird navigation a group from Cornell University, based at the Arctic Research Laboratory at Point Barrow, spent the summer of 1948 studying birds in arctic Alaska.

Figure 3A. Dr. R. J. Hock places Geiger counter near nest of semi-palmated plover, whose eggs are camouflaged to resemble pebbles. The cable is later buried and the box containing the recording meter is concealed. Figure 3B shows record obtained with this mechanism. Fluctuating baseline shows natural background radiation level, and the abrupt rise at 21 hours and 29 minutes shows the precise moment of the bird's return.



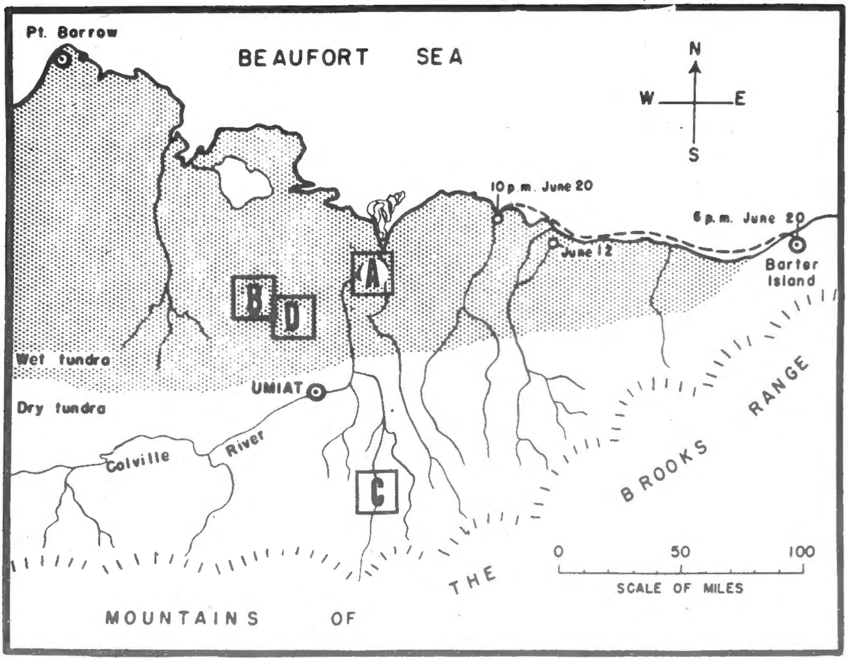


Figure 4. Map of arctic coastal plain of Alaska. A, B, and C are points where semipalmated plovers were released to test their ability to find their way home to their nests at Umiat. Also shown are the points where a large flock of snow geese was observed and the distance evidently flown by these birds during four hours of non-migratory cruising.

Semipalmated plovers (Charadrius hiaticulatus semipalmatus), nesting at Umiat on the Colville River, proved well suited to homing experiments, except that the number of nesting pairs accessible to us was too small to permit homing experiments on the scale desirable. The few birds available, however, gave results comparable to homing experiments in temperate latitudes.

Since the birds would have been frightened by observers watching too close to their nests, a different method of recording their movements was devised. Harmless radioactive tags were attached to them. Then Geiger counters were placed near the nests and records of background radiation made. An increase in radiation indicated return of the birds (see Figures 2, 3A and 3B).

Figure 4 shows Umiat relative to the Arctic Ocean and the Brooks Mountain Range. The plovers used for these experiments probably had reached Umiat by flying through one of the passes in this range of mountains, according to studies made by Dr. L. Irving and his associates. For this reason, we believe that the coast of the Arctic Ocean and a strip of territory between the ocean and Umiat had not been visited by these birds. When one plover was taken to point A, in the unknown territory (55 miles NE of Umiat on the Colville River) it required 14 hours to return. Yet this same bird returned in only 5-1/2 hours when released at point C, a comparable distance away, at a point on the Anuktuvuk

River, 49 miles SE of Umiat. It seems likely that the striking improvement of homing speed could be due to familiarity with the terrain, since the species of bird used is one found in heavy migrations through the valley of this river. Another experiment seemed to prove the same point. A few miles north of Umiat, the tundra changes from a dry, rolling, prairie-like terrain to a flat area broken by lakes and ponds so numerous and so similar in shape that pilots find the terrain extremely difficult for contact flying. So, apparently do the plovers; for three of them, released 33 and 48 miles NW of Umiat in this area took 10, 21 and 35 hours to return. The ten-hour flight was made on the only clear day when the snowcapped Brooks range would have been visible.

Despite the numerical inadequacies of the experiment and some possible complications caused by poor visibility, it suggests that homing by birds which nest in the Arctic is not much different from that displayed by many species studied in temperate latitudes. The question deserves a more conclusive answer based upon extensive experiments.

In addition to the evidence that birds have a well developed visual memory, it is important to realize how wide-ranging are many of the larger species. This was brought to our attention in striking fashion during the summer of 1948 when we made flights over much of the Arctic looking for nesting birds for homing experiments. We noted one flock of snow geese which were not migrating but were merely cruising along the coast in search of food or nesting sites. From observing them at various points, we concluded that they had covered 120 miles in four hours or less. When we allow for the age which ducks, geese, and other large birds are known to attain, it is easy to imagine that in a few years they become familiar with a great expanse of territory.

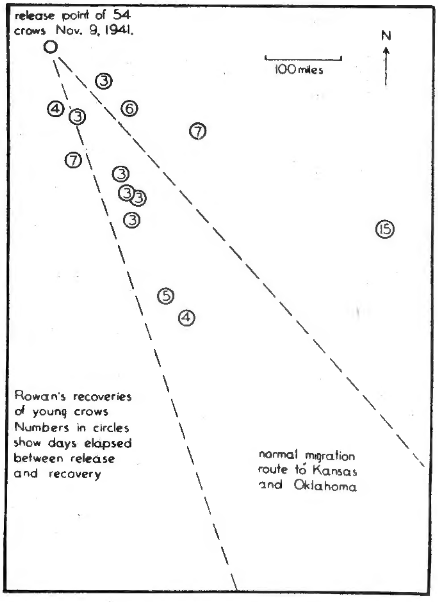


Figure 5. Map of experiment performed by Rowan which showed that young crows could migrate in the correct general direction even after being held in captivity until all adults of species had migrated southeast.

Yet visual landmarks can hardly explain the migratory flights of young birds not guided by adults. We have some rather interesting evidence on these migrations. Several weeks after all the adult wild crows from a certain section of Alberta had migrated southeast to their winter range (known from recoveries of banded birds) Rowan (1946) released some young crows. The intensive local publicity accompanying the release resulted in several reports and recoveries of the young birds at the points indicated in Figure 5. The number within each circle represents days elapsed between release and capture. In a similar experiment performed many years ago with white storks the young birds flew in directions roughly equivalent to their normal migration but

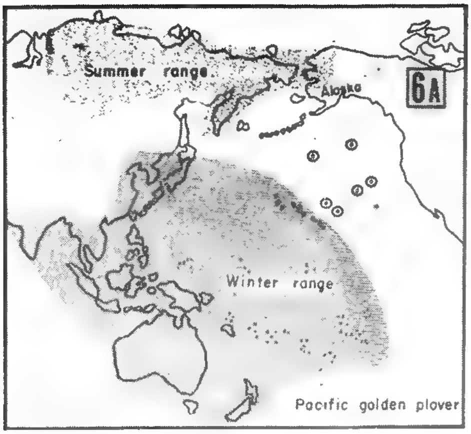


Figure 6A. Migration of Pacific golden plover (6B) from a summer range in Siberia and northwest Alaska to a winter range in the southwest Pacific. Records of this species sighted from ships in the northwest portion of the Pacific are indicated by the symbol ⊙, showing that several birds were not flying a direct course.

deviating sometimes by 30 to 40 degrees (Schuz, 1949). Still another experiment involved capturing adult hooded crows as they passed through an area on the coast of the Baltic Sea, and transporting them west to Flensburg where they were released to continue their spring migrations (Rüppell, 1944). All but one of these recoveries lay to the north and east of Flensburg, in an area roughly the size of the normal summer range, but displaced westward. It appears that the crows continued in the normal direction of their spring migration but flew into Denmark instead of into the Baltic States and Finland.

These three experiments and the one involving the gannets suggest a concept of migration which is different from that ordinarily presented. Clearly, there must be some factor, not yet understood, which guides migrating birds in the right general direction. But it seems that this guidance may not be as precise as we have often believed. The three experiments with young migrants, for example, showed a tendency for the routes to be scattered over an angle from 30 to 90 degrees. If it were true that bird migrations were guided only with this degree of accuracy then at least it would not be necessary to explain a pin-point type of navigation. It has often been argued that, because birds frequently return hundreds of miles to breed in the same small area or even at the same nesting site, they must be able to set a very precise course from their winter range. But if the birds have well developed visual memories and can use exploration at the end of the flight to determine where they will stop, there would be no need for such precision. We know, in fact, of no case where a bird steers a straight course for a distant goal across trackless areas.

Spectacular cases where precise navigation has seemed necessary are the annual flights of many birds to small islands. The Pacific golden plover (Figure 6, A and B), for instance, migrates from the arctic tundra where it nests, through the Alaskan Peninsula and the Aleutian Islands to a winter range which includes almost all the islands of the Pacific Ocean. In the case of those birds which fly to the Hawaiian Islands, it has been argued that they must use precise navigation to cross 2000 miles of open sea and yet strike an island which is only a few miles

wide. Since the golden plovers apparently do not rest on water and hence must make the journey non-stop this has always appeared to be one of the most impressive and mysterious cases of migration (Henshaw, 1915).

But actually we have no banding evidence to tell us that the golden plovers from any one point in the summer range tend to fly to a particular Pacific Island. Moreover, only the extreme western edge of the summer range lies in Alaska; the birds are also found nesting in a large section of Siberia. And in the winter they have been reported not only from Pacific Islands but also from New Zealand, Australia, the West Indies, Japan, China and India. This range is a large target, and we have no reason to think that the birds are particularly selective about the portion of it that they fly to.

Nevertheless, there is a marked migration of these plovers over the Alaska Peninsula and the Aleutian Islands. These birds apparently head out over the Pacific and some of them stop on the closest land they can reach--the Hawaiian Islands. We have some evidence (not by any means conclusive), derived from records of plovers sighted by ships in the NE Pacific, which indicates that the course flown by many of these birds over the ocean is anything but a straight line between the starting points and the goal of the migration.

In the light of the evidence, it seems that we should focus our search for the basis of bird navigation not upon some hypothetical built-in physiological instrument capable of setting very precise courses, but upon something which could guide a migrating bird in the right general direction, plus or minus perhaps 20 to 30 degrees. What environmental factors could guide migrants to this degree? Our meagre knowledge of birds' behavior during migration leads to speculation. But a few factors are at least worthy of further study. Wind direction, for example, at altitudes of 2000 feet or more is less variable than it is at the earth's surface. One investigator (Lowery, 1950) has noted a high correlation between the direction of winds aloft and the direction of nocturnal bird migrations, observed through a telescope against the illuminated surface of the moon. Cloud formations also may be stable enough in some areas to afford guidance over what might at first seem to be trackless areas.

Other possibilities that should not be overlooked as possible celestial landmarks, are the sun and moon, for we know that insects--the honeybee, for example (Frisch, 1950)--set flight courses rather accurately by means of the sun's position. Both the sun and moon appear to observers in northern latitudes to lie well south of the zenith and thus offer a limited degree of guidance.

We do not know if any of these factors are actually recognized by birds. We do know that their senses are adequate to detect them all. Obviously more studies are needed before we can arrive at any definite conclusions. Fortunately modern technological advances may help us with one problem--the need to learn more about the actual routes flown by migrating birds. We should find out, for example, how direct and accurate a course they are able to steer, and determine the relative importance of contact flying, guidance by geographical clues (coastlines, river systems and mountains), and atmospheric conditions (wind and visibility). Probably following the birds in planes is not the ideal way

to get such information and a new method may have to be devised. Another aspect of the research will be to test the hypothesis that the Alaska summer gives the birds a major advantage by permitting a shorter nesting period. This can be done by making comparisons of growth rates of the same species nesting at high and low altitudes, and of the mortality during this period of their lives.

Studies like these must be regarded as fundamental biology. But even though concrete results cannot be foreseen at present, scientific history should make us cautious in predicting that practical applications will not eventually be forthcoming. Until they are, however, we must just regard our research as a quest for understanding of a major biological problem. Certainly it is a fascinating one and a mystery that has intrigued men throughout the ages. I suggest that the phenomenon of bird migration be born in mind by readers during air travel when visual contact with the ground is obstructed by darkness or by clouds. It is at such times that the accurate navigation of these "citizens of the sky" most strongly arouses our intellectual curiosity, admiration and respect.

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